Chapter

Abiotic Stress-Induced Molecular and Physiological Changes and Adaptive Mechanisms in Plants

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Abstract

Abiotic stress is the primary cause of crop loss worldwide, reducing average yields for most major crop plants by more than 50%. Among abiotic stress, drought, salinity, high temperature, and cold are major adverse environmental factors that limit the crop production and productivity by inhibiting the genetic potential of the plant. So, it leads to complete change of morphological, physiological, biochemical, and molecular behavior of the plants and modifies regular metabolism of life, thereby adversely affecting plant productivity. Major effects of the drought, salinity, extreme temperatures, and cold stress are often interconnected and form similar cellular damage. To adopt plants with various abiotic stresses, plants can initiate a number of molecular, cellular, and physiological changes in its system. Sensors are molecules that perceive the initial stress signal from the outside of the plant system and initiate a signaling cascade to transmit the signal and activate nuclear transcription factors to induce the expression of specific sets of genes. Understanding this molecular and physiological basis of plant responses produced because of abiotic stress will help in molecular and modern breeding applications toward developing improved stress-tolerant crops. This review presents an overview and implications of physiological and molecular aspects of main abiotic stress, i.e., drought, heat, salt, and cold. Potential strategies to improve abiotic tolerance in crops are discussed.

Keywords: abiotic stress, signal transduction, stress-inducible genes, gene expression, mitigation process, genetic engineering and genome editing

1. Introduction

Plants live in constantly changing environments that are often unfavorable or stressful for growth and development. These unfavorable environmental conditions for plant growth are drought or water stress, high temperature or heat stress, low temperature or cold stress, excessive salt or salinity stress, and heavy metals toxicity like aluminum, arsenate, and cadmium in the soil. These adverse abiotic stresses are major threat that limits agriculture production and productivity, thereby creating great food insecurity. In the near future, it is predicted that because of climate change, abiotic stresses may become more intense and frequent. Drought and salinity are becoming drastically increased in many regions and may cause serious salinization of more than 50% of all arable lands by the year 2050. Consequently, because of rising temperatures and frequent flooding events for several decades,

fertile agricultural land and crop yields may decrease rapidly, especially in the mid-latitudes [1, 2]. In addition to these factors, anthropogenic activities may lead to an increased abundance of soil, water, and air pollutants, factors that plants must cope with. Moderate estimates propose that more than 90% of the land in rural areas is affected by abiotic stress factors at some point during the growing season [3]. On the other hand, the population explosion has resulted in a higher demand for food and other natural resources.

Thus, understanding stress responses is essential when attempting to develop stress-resistant cultivars that can withstand abiotic stressors and in order to feed the growing population. Plants, which undergo various abiotic stresses, sense the enormous stress signal in order to respond to the stress condition. The primary signal caused by drought is hyperosmotic stress, which is often referred to simply as osmotic stress, and salt stress has both osmotic and ion toxicity effects in cells. The secondary effects of drought and salt stresses are complex and include oxidative stress; damage to cellular components such as membrane lipids, proteins, and nucleic acids; and metabolic dysfunction. Thus, drought and salt have unique and overlapping signals. Salt and drought stress disrupts homeostasis in water potential (osmotic homeostasis) and ion distribution (ionic homeostasis). This disruption of homeostasis occurs at both the cellular and the whole plant levels. Drastic changes in ion and water homeostasis lead to molecular damage, growth arrest, and even death. While some cellular responses are induced from primary stress signals, others arise mainly from secondary signals. An important feature of drought and salt stress is that the hyperosmotic signal causes the accumulation of the phytohormone abscisic acid (ABA), which in turn elicits many adaptive responses in plants [4]. Cold or chilling stress affects plant growth and development, by changing the cell structure. First, symptom of cold stress is changing the cell membrane structure in plants; this event initiates primary cold stress responses in plants [5]. Second, chilling stress disturbs the stability of proteins or protein complexes and reduces the activities of enzymes such as ROS scavenging enzymes. These processes result in photo-inhibition and impaired photosynthesis, as well as considerable membrane damage [6, 7]. Third, chilling stress affects gene expression and protein synthesis, as it favors the formation of secondary structures in RNA [8].

To achieve stress tolerance, three interconnected aspects of plant activities are important. First, damage must be prevented or alleviated. Second, homeostatic conditions must be reestablished in the new, stressful environment. Third, growth must resume, even though at a reduced rate [9]. Significant progress has been made in understanding the physiological, cellular, and molecular mechanisms of plant responses to environmental stress factors [10]. The detection of a stressful condition results in variations in gene expression, causing changes in the composition of plant transcriptome, proteome, and metabolome. Responses to stress are not linear pathways, but are complicated integrated circuits involving multiple pathways and specific cellular compartments, tissues, and the interaction of additional cofactors and/or signaling molecules to coordinate a specified response to a given stimulus [11]. With advancement of omic technologies, i.e., genomics, transcriptomics, proteomics, and metabolomics, now it is possible to analyze and identify the most complicated interlink between various stress response, signal transduction, gene expression, and metabolites production in plants with respective to the abiotic stress [12, 13].

2. Crop plants and abiotic stresses

Generally, many stress factors act at same time, such as the frequently combined, heat, water, and high-light stress [14]. Abiotic stress changes the expression

pattern of the various genes in crop plants. So, this modification affects the regular function of plant metabolism, and source-sink relationship in turn reduces the growth, production, and productivity.

2.1 Drought

Distribution of rainfall is uneven due to the change in climate, which acts as an important stress as drought. Drought is the main abiotic stressor around the world and drastically reduces grain yields. It devastatingly influences the capability to meet the food demands of an ever-increasing global population. Drought stress is associated with water deficit and cellular dehydration. Plant adaptation to drought is a trait involving morphological, physiological, and biochemical changes. Plants reduce their growth of shoots under drought conditions and reduce their metabolic demands. Reduction in yield by as much as 40% was observed for maize and 21% for wheat at approximately a 40% water reduction [15]. In the case of cowpea, yield reduction can vary between 34 and 68% depending on the developmental timing of the drought stress [16].

2.2 Heat or higher temperature

Plants are more sensitive to the temperature conditions; in extreme cases, the unfavorable temperature condition leads to plant death. Normally plant growth and function would be better at optimum temperature level; both conditions below and higher temperature than optimum temperature severely affect the plant growth and production. The rate of most biochemical, enzymatic reactions rises two-fold for every 10°C increase between 20 and 30°C. Temperatures outside this range reduce the reaction rate because enzymes become either inactivated gradually or denatured.

Change of a few degrees considerably affects the plants' growth and development, especially reproduction. Abiotic stresses, specifically high and low temperatures, have a harmful effect on the early stage of male gametophyte in several agricultural crops such as rice, wheat, maize, barley, sorghum, and chickpea [17]. Male sterility and abnormalities in the spikelets' production were induced by heat stress in rice and wheat [18]. In both wheat and rice, heat and cold stresses caused tapetum degradation, microspore callose wall and exine formation, and changes in carbohydrate metabolism, eventually resulting in male sterility [19]. By contrast, temperature stress has no negative effect on female gametophyte development [20].

2.3 Salt

Soil salinization is a major threat to agriculture in arid and semi-arid regions, where water scarcity and inadequate drainage of irrigated lands severely reduce crop yield. More than 6% of the world's total land area and out of 230 M ha of irrigated land 45 M ha (19.5%) is already affected by salt [21]. Salt accumulation inhibits plant growth and reduces the ability to uptake water and nutrients, leading to osmotic or water-deficit stress. Salt stress tolerance level varies from one species to another. For cereal crops, barley (*Hordeum vulgare*), the most tolerant cereal, can tolerate up to 250 mM NaCl (equivalent to 50% seawater) and bread wheat is a moderately salt-tolerant crop, whereas rice, durum wheat (*Triticum turgidum* ssp.), maize (*Zea mays*), and sorghum (*Sorghum bicolor*) are less tolerant to salinity [22]. The reduction in plant growth following salt exposure is due to two phases, osmotic stress and ionic toxicity [23].

2.4 Cold

Cold stress has proved to be the main abiotic stress that decreases productivity of agricultural crops by affecting the quality of crops and their postharvest life. Cold stress, including chilling (0–15°C) and freezing (<0°C), is an abiotic stress that adversely affects the growth and agricultural productivity of plants [24, 25]. Freezing stress is highly detrimental to plants when compared with chilling stress. Usually, freezing damage will start with formation of ice nucleation in between the cell, then slowly grow and form ice crystals, and induce water leakage, leading to cell dehydration [26, 27]. However, many important crops are still incompetent to the process of cold acclimation. Rice (*Oryza sativa*), maize (*Zea mays*), tomato (*Solanum lycopersicum*), soybean (*Glycine max*), and cotton (*Gossypium hirsutum*) lack the ability to acclimate to cold temperatures and can only grow in tropical or subtropical regions [28]. Thus, cold stress adversely affects plant growth and development, limits the geographical distribution of plant species, and decreases crop yields worldwide [26].

3. Stress and crops

Stress refers to any substance or stimulus that restricts plant metabolism, growth, development, and crop productivity, including biotic and abiotic stresses [29]. Once this threshold is surpassed, an organism is stressed and mechanisms are activated at molecular, biochemical, physiological, and morphological levels. The activation of the mechanisms can result in the establishment of a new physiological state and homeostasis is reestablished [30]. Stress-related alterations in plant development, growth, and productivity reduce yield and cause unacceptable economic losses in agriculture. It has been assessed that abiotic stresses may reduce up to 70% of crop production of many economically important crops and perform at only 30% of their genetic potential with respect to yield [31].

4. Abiotic stress sensing and responding mechanism in plants

Sensors are biological molecules that recognize the adverse environmental modification and evoke the immediate response to the particular environment change by initiating the signal molecules in the system. Drought, salt, and cold stresses are inducing more amount of Ca^{2+} entry into the cell cytoplasm from internal stores or apoplastic source. Passages controlling Ca^{2+} entry are considered as one type of sensor for the stress signals [32–34]. Other than Ca^{2+}, ROS and nitric oxide (NO) are other messenger molecules involved in inducing plant response to cold stress. Reactive oxygen species (ROS) like superoxide ($O_2^{\cdot -}$), hydroxyl radicals (OH^-), and hydrogen peroxide (H_2O_2) are produced in plants in order to face various stresses [35]. Receptor-like kinases (RLKs) have an extracellular domain in which ligand is binding or protein-protein interaction will occur, a transmembrane domain, and an intracellular kinase domain. When the ligand or signal binds extracellular domain, histidine residue present in the intracellular kinase domain is auto-phosphorylated and the phosphoryl moiety is received by aspartate receiver part of the sensor protein or a separate protein. Then, the activated sensor protein(s) may induce cellular responses specific to signal through the mitogen-activated protein kinase (MAPK) cascade or directly phosphorylate specific targets. Intracellular signaling mode, i.e., protein

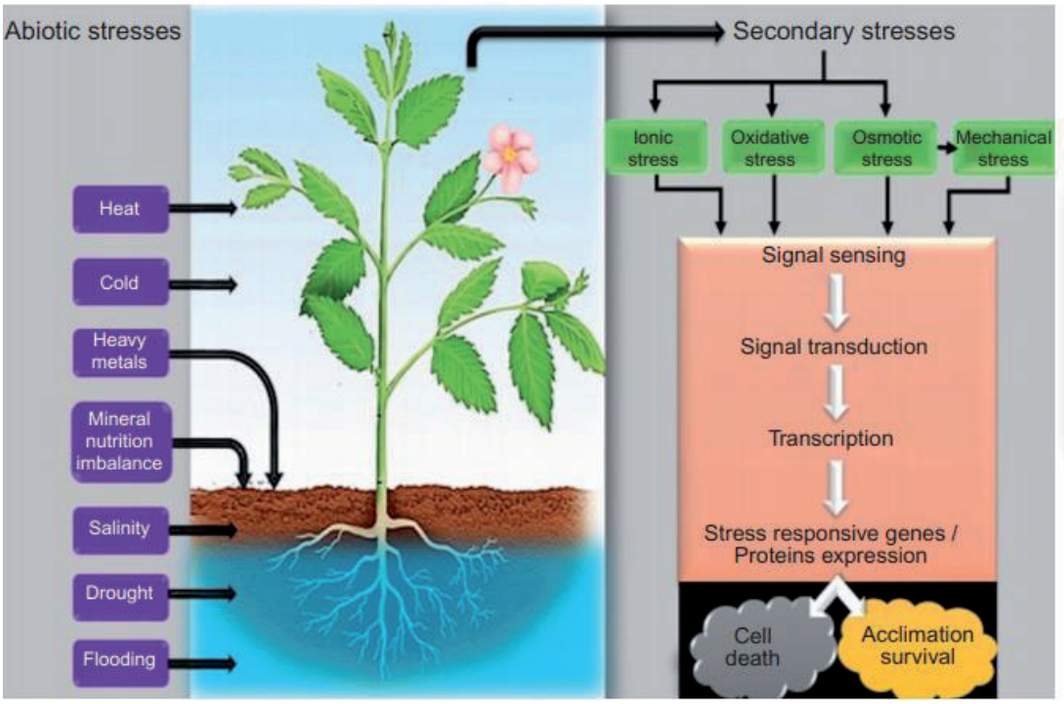

Figure 1.
Plant responses to abiotic stress.

phosphorylation and dephosphorylation regulate a wide range of cellular processes such as enzyme activation, assembly of macromolecules, protein localization, and degradation [36]. Upon sensing of abiotic stress by plants, signaling cascades are induced that activate ion channels, kinase cascades, assembly of reactive oxygen species (ROS), and accumulation of plant hormones leads to induce expression of specific subsets of genes that responsible to combat the abiotic stress (**Figure 1**) [37].

5. Similar and variable features of drought, salt, and cold stress

All the three stresses such as drought, salt, and cold stresses cause a primary loss of cell water, which leads to decrease in cell osmotic potential but the reason of cell water loss varies among stresses: (i) the decrease of the cell water content under drought stress is due to water shortage in soil or/and in the atmosphere. (ii) In salt stress, osmotic or water potential of surrounding root zone is decreased by Na^+ and Cl^- solutes, which in turn create more difficulty in uptake by roots and water translocation to metabolically active cells; (iii) osmotic stress is created in cold stress mainly because of inability to transport the water available from the soil to the living cell of leaf mesophyll. This condition is called as physiological drought. Anyhow, water loss in cell increases abscisic acid (ABA) biosynthesis, and it is well-known fact that it is involved in activation of various drought, salt, and cold stresses, responsive genes in plant system [38]. In plant system losing of cell water and increasing of solute concentration (especially Na^+) by these three stress cause lower osmatic potential and it creates harmful effects to the protein and enzymes. This effect can be avoided by producing more amounts of low molecular osmolytes (carbohydrates [39], betaine [40], and proline [41]) that can counteract cellular dehydration and turgor loss [42]. Production of low molecular osmolytes in higher quantity is a common stress alleviating process for drought, cold, and salt stress. While main cause of drought stress is osmotic, Na^+, ion toxicity, for salt stress,

and physiological drought for cold stress, all stresses have an influence on most biochemical reactions such as photosynthesis, carbon metabolism reactions, and enzyme activities.

6. Gene expression and regulation under abiotic stress

Expression of a variety of genes in plants is induced by environmental stresses such as drought, high salinity, and low temperature. Upon expression, various proteins are produced in various parts of the plants, which not only protect the cell but also initiate humpty number of genes which are responsible for inducing various abiotic resistance mechanisms in plants. Different types of proteins, i.e., chaperones or late embryogenesis abundant (LEA) proteins are produced mainly involved to create tolerance, whereas stress-responsive genes are all involved in to generate stress response [43]. The regulation of stress-responsive plant genes at three levels: transcriptional, posttranscriptional, and posttranslational.

6.1 Gene regulation at transcriptional level

Transcriptional regulation involves (i) chromatin and its alteration and remodeling; (ii) cis-regulatory elements such as enhancers and promoters, which are often binding sites, located upstream and downstream the coding region; and trans-regulatory elements, usually transcription factors. Different environmental stresses create altered methylation pattern of DNA and changing histones protein in order to suppress or increase the transcription of the gene.

Promoters are specific sequences involved in regulatory function, where they bind RNA polymerase and different transcription factors to start the transcription [44]. Dehydration-responsive element-binding (DREB) or C-repeat binding factor (CBF), MYB, basic-leucine zipper (bZIP), and zinc-finger families are some of the trans-regulatory elements involved in the regulation of plant defense and stress-responsive genes upon binding in cis element of the respective gene promoters [45]. Overexpression of the *Oryza sativa* WRKY11 (transcription factor or trans-regulatory elements) under the control of heat shock protein 101 (HSP101) promoter led to enhanced drought tolerance [46, 47]. The important discovery of a novel *cis*-acting element, C-repeat/dehydration response element (CRT/DRE), is responsive to drought, cold, and high-salt stress [48]. Since this discovery, CBF proteins have been isolated sequentially by screening for DNA-binding proteins that bind to the CRT/DRE motif [49, 50]. *Arabidopsis* contains three cold-induced *CBF* genes, *CBF1–3* (*CBF1/DREB1B*, *CBF2/DREB1C*, and *CBF3/DREB1A*), which are arranged in tandem on chromosome IV. CBF 1–3 are APETALA2/ETHYLENE-RESPONSIVE (AP2/ERF1)-type transcription factors that directly bind to the conserved CRT/DRE motifs in the promoters of *COR* genes (known as CBF regulons) and activate their expression under cold conditions [50–52]. Transgenic *Arabidopsis* plants overexpressing *CBF1* display increased *COR* expression and enhanced freezing tolerance [53]. *CBF* orthologs have been isolated in many plant species, including rice, tomato, wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), and maize [54]. Heterologous expression of *Arabidopsis CBFs* enhances freezing tolerance in various species, and heterologous expression of *CBFs* from other plant species enhances freezing tolerance in *Arabidopsis* [55–57]. Cold-sensitive tomato (*Lycopersicon esculentum*) become freezing tolerant upon overexpression of its own *CBF* genes, i.e., *LeCBF1*; however, overexpression of cold-tolerant *Arabidopsis CBF3* in tomato plants do not exhibit freezing tolerance; this proves that there are different CBF regulons

in tomato and *Arabidopsis* [56]. It also indicates that the biological function of *CBF1–3* in modulating freezing tolerance is not only highly conserved among plants but also species specific.

6.2 Gene regulation at posttranscriptional level

Regulation that occurs in the stage of pre-mRNA till translation of mRNA is called posttranscriptional gene regulation. It occurs in four stages: (i) pre-messenger (mRNA) processing (capping, splicing, and polyadenylation), (ii) mRNA nucleocytoplasmic trafficking, (iii) mRNA turnover and stability, and (iv) mRNA translation [58]. One more strategy, i.e., alternative splicing (AS) is regulating the gene under cold and heat stress. STABILIZED1 (STA1), a gene coding for a nuclear pre-mRNA, is one of the best examples for alternate splicing factor which is involved in cold stress resistance in *A. thaliana* [28, 59]. Posttranscriptional regulation also is important for *COR* gene function. *REGULATOR OF CBF GENE EXPRESSION1* (*RCF1*), encoding a DEAD-box RNA helicase, helps ensure the proper pre-mRNA splicing of many *COR* genes under cold stress [60]. *STABILIZED1* (*STA1*) encodes a pre-mRNA splicing factor that controls the pre-mRNA splicing and mRNA turnover of *COR* genes [59]. Genome-wide AS profiling analysis revealed that hundreds of genes such as *RCF1* and *STA1* that have highly altered AS in the first few hours of cold treatment. This study showed that plant using AS pathway to change the gene expression in order to respond the temperature stress [61, 62]. Small RNAs (20–25 nucleotides) are processed from noncoding double-stranded RNA precursors by RNAses of the DICER-LIKE (DCL) family and mediate a series of gene silencing mechanisms at posttranscriptional level. One of these mechanisms cleaves mRNAs or prevents their translation through the mediation of 21 nucleotide microRNAs [63–65].

6.3 Posttranslational level regulation

Phosphorylation, sumoylation, and ubiquitination of proteins are posttranslational-level processes that play vital roles in the changing of plant response to various abiotic stresses. Mitogen-activated protein kinases (MAPKs) and SNF-1-relatedprotein kinases (SnRKs) are formed numerous signal transduction cascades, induced by dehydration and osmotic stress through the phosphorylation of specificresidues [66]. XERICO controls the level of ABA by enhancing the transcription of the key ABA biosynthetic gene AtNCED3. SnRK2 proteins and XERICO gene, encoding a H2-type zinc-finger E3 ubiquitin ligase, are involved in ABA-dependent responses to water deficit, like stomata closure [67–69].

Posttranslational histone modifications, along with DNA methylation, are associated with gene expression levels in response to cold stress. Histone acetylation/deacetylation catalyzed by histone acetyltransferases (HATs) and histone deacetylases (HDAs) plays a role in cold responses in plants [70]. *Arabidopsis HISTONE DEACETYLASE6* (*HDA6*) is upregulated by cold stress and positively regulates freezing tolerance [71]. *HDAs* also are upregulated by cold stress in maize, leading to global deacetylation at H3 and H4. Under cold stress, HDAs appear to directly activate maize *DREB1* (*ZmDREB1*) expression and histone hyperacetylation. Histone acetylation of *OsDREB1b* in rice and *ZmDREB1A* and *ZmCOR413* in maize is induced by cold stress [72, 73]. RNA-DIRECTED METHYLATION4 (RDM4) protein was reported to function in RNA-directed DNA methylation (RdDM) by working with RNA polymerases Pol V and Pol II in *Arabidopsis* [74]. Under cold stress, RDM4 is important for Pol II occupancy at the promoters of *CBF2* and *CBF3* genes [75].

7. Important signal transduction pathway for drought cold and salt

Abiotic stresses such as cold, drought, and salt inducing signal transduction networks are divided into three types: (I) osmotic/oxidative stress signaling that uses MAPK modules to generate ROS scavenging enzymes, antioxidant compounds, and osmolytes; (II) Ca^{2+}-dependent signaling helps to activate late embryogenesis abundant (LEA)-type genes (such as the DRE/CRT class of genes), and (III) Ca^{2+}-dependent salt overlay sensitive (SOS) signaling that regulates ion homeostasis (**Figure 2**) [14, 76].

7.1 Oxidative or osmatic stress signaling

Formation of reactive oxygen species (ROS) such as superoxide, hydrogen peroxide, and hydroxyl radicals is common for all the stresses, particularly drought, heat, salt, cold, and oxidative stress. Reactive oxygen species which are produced by the environmental stresses cause major plant damage (oxidative stress) [77]. High amount of ROS acts as a signal, and synthesizing ROS scavengers is one of the protective mechanisms in plants. Osmotic stress stimulates many protein kinases; among them, one is mitogen-activated kinases, which are involved in

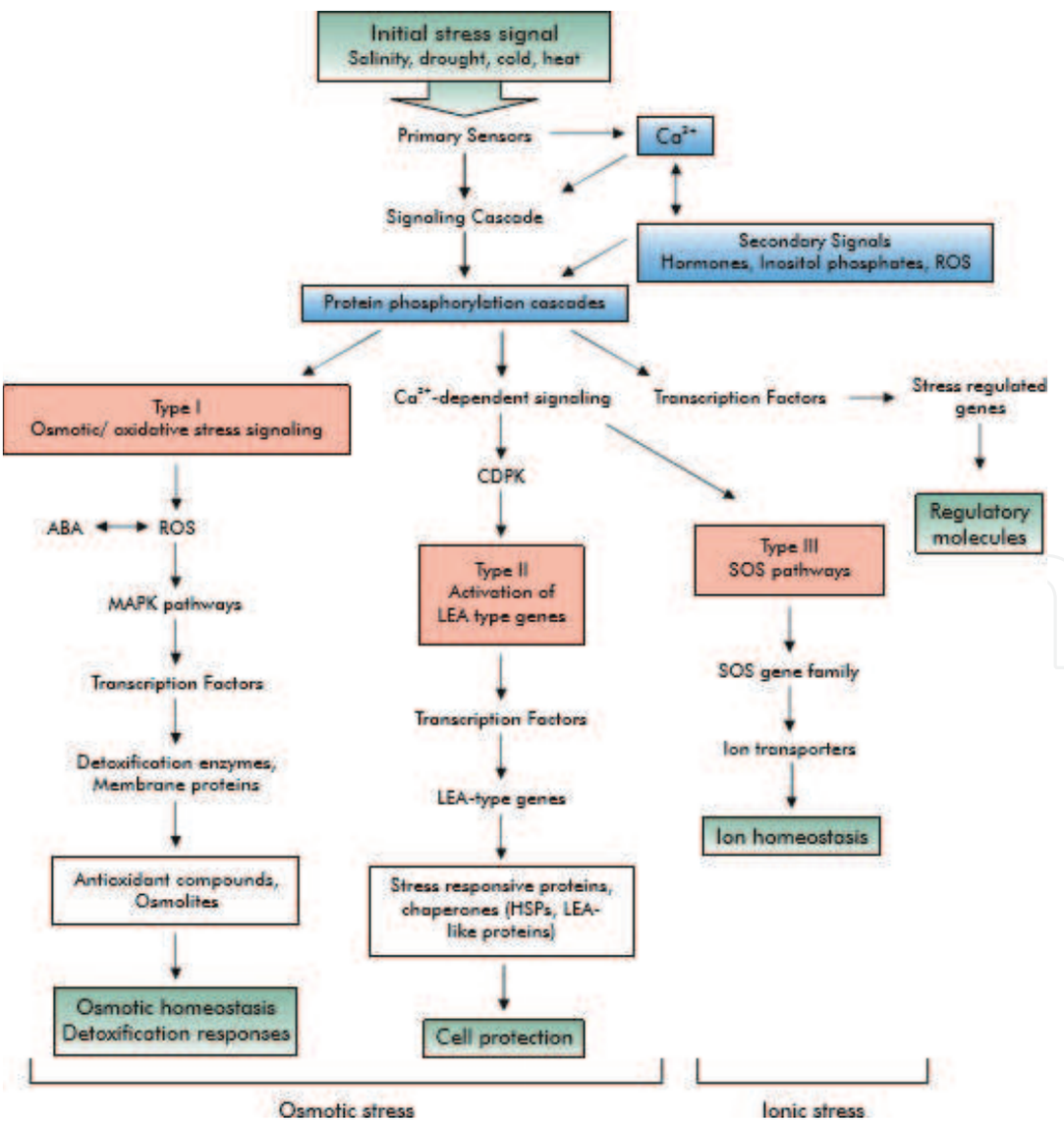

Figure 2.
Schematic pathway for the transduction of osmotic and ionic stress in plants.

reestablishing the osmotic homeostasis. Plant cells which undergo osmatic stress should produce more osmolytes in order to mitigate the negative effect of the ROS and maintain the osmotic homeostasis. So, the osmotic stress activate the receptors/sensors proteins such as protein tyrosine kinases, G-protein-coupled receptors, and two-component histidine kinases; this will trigger MAPK pathway and signal cascade, which is responsible for production of more amount of osmolytes that are necessary for osmotic adjustment. The main purpose of osmolytes is to maintain cell turgor, thus the driving gradient for water uptake. Compatible solutes such as amino acids (e.g., proline), quaternary amines (e.g., glycine betaine and dimethyl sulfoniopropionate), and polyol/sugars (e.g., mannitol and trehalose) will act as free radical scavengers or chemical chaperones by directly stabilizing membranes and proteins [78].

The MAP kinase pathways are intracellular signal modules that mediate signal transduction from the cell surface to the nucleus. The core MAPK cascades consist of three kinases that are activated sequentially by an upstream kinase. The MAP kinase kinase kinase (MAPKKK), upon activation, phosphorylates a MAP kinase kinase (MAPKK) on serine and threonine residues. This dual-specificity MAPKK in turn phosphorylates a MAP kinase (MAPK) on conserved tyrosine and threonine residues. The stimulated MAPK either travels to the nucleus to stimulate the transcription factor directly, or activates additional signal components to regulate gene expression, cytoskeleton-associated proteins or enzyme activities, or targets certain signal proteins for degradation [14].

7.2 Ca^{2+}-dependent signaling to activate late embryogenesis abundant (LEA) genes

Abiotic stress induces more Ca^{2+} entry into the cell cytoplasm; channels which control the Ca^{2+} entry act as a sensor for these abiotic stress signals. Ca^{2+} activates the calcium-dependent protein kinases (CDPKs), and CDPKs are serine/threonine protein kinases with a C-terminal calmodulin-like domain with four EF-hand motifs that can directly bind Ca^{2+}. CDPKs are encoded by multigene families, and the expression levels of these genes are spatially and temporally controlled throughout development. CDPK pathway is involved in production of high amount of anti-desiccation protection protein (LEA proteins) by activation of LEA-type genes including the dehydration-responsive element (DRE)/C-repeat (CRT) class of stress-responsive genes. Activation of LEA-type genes actually represents damage repair pathways but this is completely different from the pathways regulating osmolyte production [79, 80]. At the time of seed maturation, naturally it undergoes desiccation; to avoid desiccation shock during seed germination, seeds accumulate more transcripts and relatively high concentration proteins; for this reason, these proteins were named as late embryogenesis abundant (LEA) proteins [81]. Water deficit, high osmolarity, and low temperature stress induce the accumulation of an LEA protein in crop plants. Such proteins are used to prevent protein denaturation or renaturing unfolded proteins, realm protein structure and membrane integrity, and sequestering ions in stressed tissues. Many scientific reports suggest that LEA proteins and chaperones are involved in protecting macromolecules such as enzymes, lipids, and mRNAs from dehydration, and these proteins have been grouped into at least six families on the basis of sequence similarity [12, 82, 83]. LEA proteins are specialized in desiccation protection of membranes; and antioxidant enzymes and molecules are involved to achieve desiccation tolerance. Both osmolytes and LEA proteins work together in stabilization of membrane and protein structures by conferring preferential hydration at moderate desiccation and replacing water at extreme desiccation [84].

7.3 Ca^{2+}-dependent salt overlay sensitive (SOS) signaling

Calcium-dependent SOS signaling regulates ion homeostasis relatively specific to the salt stress. Ion transporters are main target for this type of signaling that controls ion homeostasis under salt stress. Excess extracellular or intracellular Na^+ acts as an input for the SOS pathway and mainly increases a cytoplasmic Ca^{2+} signal, and this signal changes expression and activity of transporters for ions such as Na^+, K^+, and H^+. The input for osmotic stress signaling is like a change in turgor. Salt stress signal transduction comprises of ionic and osmotic homeostasis signaling pathways, detoxification (e.g., damage control and repair) response pathways, and pathways for growth regulation [66]. This signaling pathway mediates salt induction of the SOS1 gene in *Arabidopsis*. In addition, the SOS2-SOS3 kinase directly phosphorylates and activates the SOS1 transporter [14, 85]. Studies comparing the growth of wild-type and mutant plants in response to NaCl and sequence analysis of the predicted SOS1 protein suggested that SOS1 encodes an Na^+/H^+ exchanger (antiporter) on the plasma membrane [86]. Because the SOS pathway operates during ionic stress, it is thought that homologs of SOS3 and SOS2 may also function in the transduction of other stress or hormonal signals [87]. Transient increases in cytosolic Ca^{2+} are perceived by various Ca^{2+}-binding proteins. In the case of abiotic stress signaling, evidence suggests that Ca^{2+}-dependent protein kinases (CDPKs) and the SOS3 family of Ca^{2+} sensors are major players in coupling this universal inorganic signal to specific protein phosphorylation cascades. It seems that calcium signaling is crucial for salt tolerance in plants [14].

Second messengers can control intracellular Ca^{2+} levels, often initiating a protein phosphorylation cascade that finally targets proteins directly involved in cellular protection or transcription factors controlling specific sets of stress-regulated genes. The products of stress-regulated genes like the plant hormones ABA, ethylene, and salicylic acid (SA) are mainly involved in the induction of stress-tolerant mechanism in plants. Salt and water-deficit stress participates in the production and activation of regulatory molecules, and to some extent, cold stress causes an increased biosynthesis and accumulation of ABA by activating genes coding for ABA biosynthetic enzymes, which can be quickly catabolized after the stress. Most of the abiotic stress-responsive genes are upregulated by ABA [88].

8. Managing abiotic stress by genetic engineering or genetic manipulation or genome editing

All over the world, abiotic stress significantly affects the production and yield potential of the crops and creates a major challenge for crop improvement sectors such as plant breeders and biotechnologists. Genetic manipulation of crops can be done to generate desirable character by so many ways. Among them, transgenic technology or genetic engineering and genome editing are the best strategies to develop abiotic resistant crops. Abiotic stress resistance in crops is possible by transgenic approach through boosting endogenous defense mechanisms by overexpressing of genes, which normally involves the synthesis of compatible osmolytes, antioxidants, polyamines, maintenance of hormone homeostasis, and modification of transporters and/or regulatory proteins, including transcription factors and alternative splicing events. Sometimes overexpression of some genes and thereby synthesizing of specific protein and metabolites will affect the normal metabolism and reducing the yield. Transgenic crop with abiotic tolerance but diminished yield potential and reduced growth is undesirable. So, it is important to analyze the functions of stress-inducible genes not only to understand the molecular mechanisms of

stress tolerance and responses of higher plants but also to improve the stress tolerance without reducing the yield potential of crops by gene manipulation. Hundreds of genes are thought to be involved in abiotic stress responses [89].

8.1 Transgenic crop technology for abiotic tolerance

Transgenic crop or genetic engineering technology has ample opportunity in development of crops with specific objectives by overexpression of responsible genes or suppression of undesirable genes. Present engineering approaches rely on the transfer of one or several genes that are either involved in signaling and regulatory pathways or that encode enzymes present in pathways leading to the synthesis of functional and structural protectants, such as osmolytes and antioxidants, or that encode stress-tolerance-conferring proteins [78]. Phytohormones such as ABA are major targets for genetic manipulation to obtain abiotic stress-tolerant crops. Overexpression of ABA biosynthetic pathway-related TFs imparts an ABA-hypersensitive response and also improves the osmotic stress tolerance in transgenic plants [90, 91]. Under moderate drought stress, during the flowering period, the yields of transgenic canola overexpressing a farnesyltransferase protein were significantly higher comparatively to the control [92]. The overexpression of TFs that control root architecture induced drought tolerance in rice and transgenic *Arabidopsis* plants by promoting root growth and thus enhancing WUE [93, 94]. Other TFs linked to WUE, such as those stimulating wax deposition in cuticle and suberin deposition [95]. Many scientific researches revealed that glyoxalase pathway is involved in enhancing tolerance to abiotic stress; so, overexpression of glyoxalase I and glyoxalase II genes enhances the various abiotic stress tolerance in plants [96–103]. Transgenic rice with overexpression of choline oxidase (codA), D-pyrroline-5-corboxylate synthase (P5CS), LEA protein group 3 (HVA1), alcohol dehydrogenase (ADH), and pyruvate decarboxylase (PDC) genes have shown improved tolerance to abiotic stress [104, 105]. Usually rice does not accumulate glycine betaine but transgenic rice with overexpression of codA gene in the chloroplast and the cytosol accumulate more amount of glycine betaine, which recovered to normal growth at a faster rate give comparatively more yield under salt and cold stress [106]. Overexpression of *Escherichia coli* trehalose biosynthetic genes (otsA and otsB) with stress-inducible promoter enhances abiotic stress tolerance in rice [107–109]. Transgenic tobacco plants overexpressing chloroplastic Cu/Zn-SOD showed increased resistance to oxidative stress caused by high light and low temperatures. Transgenic tobacco plants expressing alfalfa aldose aldehyde reductase, a stress-activated enzyme, showed reduced damage when exposed to oxidative stress and increased tolerance to heavy metals, salt and dehydration stress. Targeting detoxification pathways are an appropriate approach for obtaining plants with multiple stress-tolerant traits [26, 110–113].

Water stress increases the formation of ROS through membrane perturbation of electron transport chains. The loss of catalase and gain of the glutathioneS-transferase/peroxidase functions in plants associate defenses against oxidative damage,which are more important in plant salt tolerance [79]. Loss of osmotic homeostasis is the important process in the abiotic stress, which affects the cell ion concentration; so, to achieve abiotic tolerance especially salt, plants should re-establish homeostasis (ionic and osmotic homeostasis) under stressful conditions. More amount of Na^+ within the cell inhibits enzyme activity and is harmful to the proteins; so, either compartmentalization of Na^+ in the vacuole or controlling of Na^+ accumulation in the cytoplasm is more important [9]. To revert ionic and osmotic homeostasis, many ion transporters act as terminal determinants. Protein AtNHX1 of *Arabidopsis thaliana*, one type of transporter, is located in cell vacuolar

membranes involving transport of excessive Na^+ ions from cytoplasm to vacuole; thereby protecting the plant from the drying effect of salt. Overexpression of the AtNHX1 gene in transgenic tomato increased the salt tolerance and also produced good quality fruit containing less Na^+ ions because the plants store the sodium in the leaf vacuoles [114]. Plant salt tolerance genes include defenses against osmotic and oxidative stresses. The genetic analysis indicates that enzymes involved in osmolyte synthesis, osmoprotecting LEA proteins, and antioxidant enzymes such as catalases and glutathione S-transferase/peroxidase are important for plant salt tolerance [79].

8.2 Genome editing technology

Despite the benefits of commercial genetically engineered plants [115] and successfully addressing abiotic stresses, still this technology is not accepted unanimously because of the negative perception of the public; so, it limits the usage of this technique to develop the abiotic resistant crop varieties. The major concern in transgenic technology might be in many cases; the source of the gene to generate transgenic crop is taken from non-related organism, i.e., microorganism and non-related plant and animal; so, this issue can be addressed in a better manner by genome editing technology. In this technique, genetic modifications are accomplished by creating minor genome changes that are comparable with changes generated through mutation breeding (conventional crop improvement method) by using chemical and physical mutagenic agents. Mutational breeding produce changes in the genome at random manner; so, the success rate or chance of obtaining desirable genotype is quite low. But in genome editing, modification is done at targeted site, by application of sequence-specific nucleases that create double-stranded breaks in the target genomic loci selected for editing; so, the success rate of obtaining desirable genotype is very high. The major genome editing tools are zinc finger (ZF) nucleases, transcription activator-like effector nucleases (TALENs), and clustered regularly interspaced short palindromic repeats (CRISPR) [116]. Many strategies or options are there to improve agronomic traits by using genome editing tools. Introduction of a premature stop codon to terminate the functional protein production or modify to a gene promoter motif to control gene expression is one of the best examples of genome editing. Genome editing techniques such as TALEN and CRISPR-Cas9 are used to introduce targeted mutations in MILDEW-RESISTANCE LOCUS (MLO) proteins in hexaploid bread wheat [117]. On the other hand, Piatek et al. used synthetic transcriptional repressor and activator to increase gene expression [118]. C-repeat binding factors (CBFs) are responsible for cold acclimation in plants. Since *CBF1–3* loci all are on the same chromosome, by traditional genetic crossing it is highly difficult to generate *cbf1,2,3* triple mutant lines. So by using genome editing tool CRISPR/Cas9, generating single, double, and triple mutants of *CBF* genes was achieved successfully. The *cbfs* triple mutants are the most sensitive to freezing stress of these different mutants under cold-acclimation treatment. RNA-seq analysis of the triple mutants revealed that the expression of *c*. 10–20% of *COR* genes is CBF dependent [119, 120]. These findings support the notion that CBFs are key regulators that play redundant roles in cold acclimation in plants.

9. Conclusion

Plants are developed with inherent adaptive mechanisms to cope up with varied and composite abiotic stresses. Now it is possible with the help of science and technological advancement to understand function of gene, gene manipulation strategy,

and plant traits development to overcome the abiotic stress. Signaling pathways have to be regarded as complex networks. Molecular analyses of the signaling factors provide a better understanding of the signal-transduction cascades during abiotic stress. A notable improvement in crop genome characterization and functional annotation of the gene will advance our knowledge in genetic manipulation (transgenic technology) and optimization of genome editing technology toward development of abiotic stress-tolerant crops. In due course, to accomplish the desired improved varieties, genome editing and transgenic approaches both should be combined with conventional and marker-assisted breeding activities. Further, identification of new adapted germplasm is also most important to guide breeding programs in target trait identification for changing scenario of climate. These combined efforts will make notable progress to face effect of climate change, especially stress such as drought, heat, and cold stress and will contribute to enhanced crop production, productivity, and thereby food security.

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